THE DISTRIBUTION OF INTERTIDAL MACROFAUNA ON THE COASTS OF ICELAND IN RELATION TO TEMPERATURE

AGNAR INGÓLFSSON

SARSIA

INGÓLFSSON, AGNAR. 1996 05 15. The distribution of intertidal macrofauna on the coasts of Iceland in relation to temperature. – *Sarsia* 81:29-44. Bergen. ISSN 0036-4827.

Records of intertidal macrofauna, mostly collected since 1974, were analysed by the use of a 10x10 km plotting system. Data have been obtained on 208 such squares of the total of 378 straddling the intertidal, or 55.0 %. Adequate data were available on 103 species. Nine of 37 obligate intertidal species (24 %) appear to reach distributional limits towards cooler seas going clockwise around Iceland from the south coast. The presence of warm springs in the intertidal extends the range of one species far beyond the main limits. There is no example of obligate intertidal species reaching distributional limits towards warmer seas within Iceland, emphasizing the non-arctic character of the intertidal fauna. Of 66 species occurring both in the intertidal and subtidal, 11 (17 %) reach distributional limits towards cooler seas in the intertidal and appear not to penetrate further subtidally, while one species (1 %) may show the reverse pattern of limits towards warmer seas. However, some 34 intertidal-subtidal species (51 %) show a more restricted distribution in the intertidal than in the subtidal, the restriction being to the warmer coastal regions in all but one instance. Low and variable air temperatures probably become critical to these species on colder coasts. Distributional limits in the intertidal, both of obligate intertidal species and of those also found in the subtidal, tended to concentrate in regions of the coasts with relatively abrupt temperature changes, while there were also instances of limits along stretches of coasts with uniform temperatures.

Agnar Ingólfsson, Institute of Biology, University of Iceland, Grensásvegur 12, IS-108 Reykjavík, Iceland.

KEYWORDS: intertidal; macrofauna; distribution; temperature; Iceland.

INTRODUCTION

Temperature has long been considered the most critical factor determining the ecological boundaries of marine species distributions (e.g. STEELE 1983). Although there is a general relationship between distribution of water temperature and distribution of species (e.g. INGÓLFSSON 1977a), anomalies are often apparent. This is to be expected, as sea temperature can theoretically limit distributions in several ways. A particular species may thus be limited in one area by summer temperature, in another by winter temperature. Seasonal fluctuations may be of paramount importance. Sea temperature can also be expected to interact with many other physical factors in complex ways, e.g. air temperature, salinity, current, productivity, exposure, sea ice etc. Fragmentary data can often be the reason for apparent anomalies, and the literature abounds with pictures of distributional patterns later proved to be erroneous as more data were gathered.

The intertidal is eminently suited for distributional studies. It is a virtually one-dimensional habitat, and the sampling effort required to obtain reliable pictures of distributional patterns is much less than for other marine habitats which are two- or three-dimensional. The intertidal is, however, an ecotone, and many species encountered there are also subtidal in habits. The interpretation of patterns emerging for these species by the study of the intertidal is different and more complex than for those species confined to the intertidal. It is therefore important to distinguish between these two groups of species as far as possible.

The aim of the present study was to examine the distributional pattern of macrofauna occurring in the intertidal of Iceland. I examine in particular the following hypotheses: (1) Several southern species will reach distributional limits towards cooler seas within Iceland, whereas northern species are, conversely, likely to reach limits towards warmer seas. (2) These limits will be concentrated at coastal regions where sharp temperature boundaries exist. (3) Species found both subtidally and intertidally will often have different distributional limits in the two kinds of habitats.

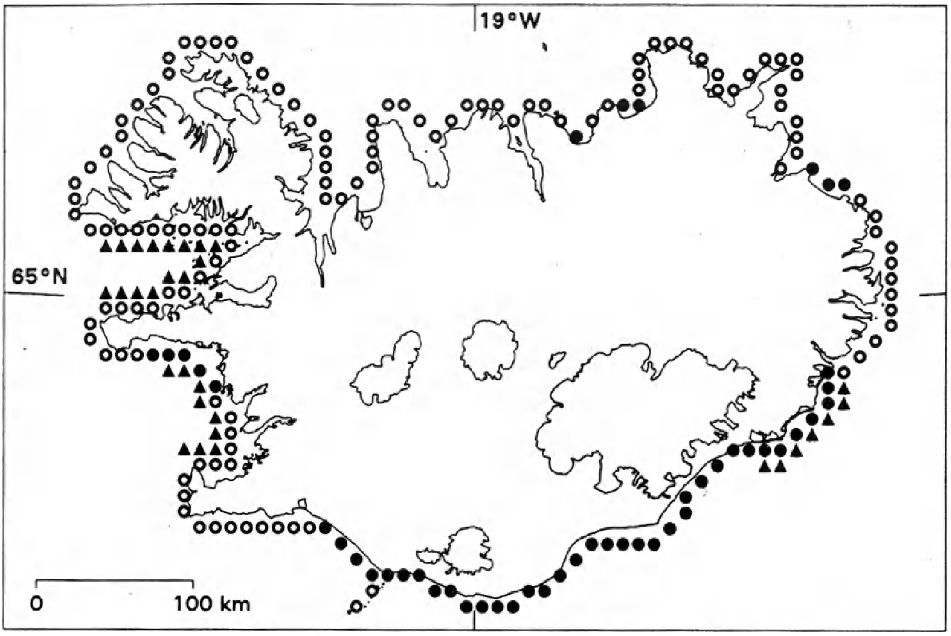

Fig. 1. The distribution of main shore types of Iceland. O : rocky shores prevalent. l : exposed sandy shores prevalent. ▲ : areas of extensive muddy tidal flats.

MATERIAL AND METHODS

Recent data on the distribution of macrofauna of Icelandic coasts have been obtained from the following sources:

(1) During 1974 and 1975 some 70 shore transects were sampled around the coasts for the study of amphipods and other malacostracans. Samples were qualitative but were taken both from rocky shores and muddy tidal flats as well as in estuaries and lagoons (see Ingólfsson 1977a for details).

(2) During summers of 1975, 1976 and 1977 more than 200 transects were sampled dispersed evenly on all coasts except for the South were few transects were investigated. Most transects were on rocky shores but tidal flats were also sampled when encountered. The general procedure on rocky shores was to put down 5-8 stations per transect with fixed height intervals. The interval used was 50 cm on southern and western coast where the tidal range is large but 25 cm on northern and eastern coasts in accord with the smaller tidal range. Animals were collected from two 20 x 20 cm squares per station. When algae were present these were cut from the squares and animals rinsed from them in the laboratory. The sites sampled ranged from very sheltered to somewhat exposed while few heavily exposed sites were investigated due to the difficulties involved. On tidal flats sampling was done at intervals along the transects without regard to vertical height. Two 20 x 20 cm squares were dug up down to 10 cm at each station and the sediments sieved with 1 mm mesh.

(3) The following surveys done in connection with various environmental issues: Garðarsson & al. 1974, 1976, 1980); Helgason & al. 1988; Ingólfsson 1976a, 1977b, 1983, 1984, 1986, 1990b, 1991; Ingólfsson & Einarsson 1980; Ingólfsson & Garðarsson 1975; Ingólfsson & Gunnarsson 1984; Ingólfsson & Helgason 1981; Ingólfsson & Svavarsson 1989; and Ingólfsson & al. 1980. Most of these surveys were done on western coasts, while there were few on northern and southern ones.

(4) The following papers treating individual species or species groups: Astthorsson 1987; Ingólfsson 1973, 1977a, 1990a; Lindroth & al. 1973; Óskarsson & al. 1977 and Solignac 1972.

(5) The following more general papers on the seashore of Iceland: Hansen & Ingólfsson 1993; Hauksson 1977; Ingólfsson 1975, 1976b, 1994.

(6) A scattering of recent (post-1980) unpublished records in the author's files.

In addition, the few pre-1960 records available from the intertidal (Larsson & Gígja 1959; Madsen 1949; Segerstråle 1947; Stephensen 1937a, 1939, 1940; Thorson 1941; Wesenberg-Lund 1951) have been taken into account when they could be pin-pointed with sufficient accuracy.

I consider the data adequate with respect to most macrofaunal groups (e.g. crustaceans, prosobranch gastropods, bivalves, polychaetes (with exceptions), echinoderms). The following groups have, however, been omitted from the analysis because of taxonomic difficulties: opistobranch gastropods, oligochaetes, most insects, nemerteans, poriferans, bryozoans, and most hydrozoans.

Nomenclature follows Hayward & Ryland (1990) when possible although different names have been used occasionally when considered more correct.

To analyse patterns the grid system of Kristinsson & Jóhannsson (1970) was employed. This system, designed for terrestrial plants, divides Iceland into 10 x 10 km squares. The number of such squares straddling the seashore is 378. None of the data here considered had been gathered with this grid system in mind, and its use therefore allows the analysis of records with the minimum of bias. This greatly outweighs any disadvantage of the system such as the varying intertidal area contained by these squares. An additional advantage was the availability of a computer program, FLORA, for plotting the records.

PHYSICAL CONDITIONS

Geomorphology

The seashores of Iceland are of three main kinds (Fig. 1): (1) Rocky shores, predominant on most coasts except the South. These shores are most extensive by far on the western coasts (Ingólfsson 1975) due to large tidal range and numerous skerries and islands. (2) Exposed sandy shores, predominant on the southern coasts, while shorter stretches are found on other coasts. (3) Muddy tidal flats. These are most extensive at the head of bays and fjords and in lagoons on the western coasts, and also in lagoons on the southeastern coast.

Tidal regimes

Tides around Iceland are semi-diurnal (Anonymous 1993). The tidal range is greatest on the middle west coast, a little in excess of 4 m at mean spring tides. The range decreases from there in both directions, but more abruptly towards the North. On many of the north and east coasts the tidal range at mean spring tides is about 1.5 m, while southern and southwestern coasts show ranges between about 2.5 and 3.8 m.

Temperatures

Nearshore surface temperatures around Iceland have been described by Stefánsson (1969) (Fig. 2). The data used are collected at varying distances from the shore and thus give only a rough indication of the sea temperatures experienced by intertidal animals. In general, the temperatures decrease clockwise around the island from a sharp temperature boundary on the southeastern coast. During winter (e.g. February) the temperature is high off the southern coast, but then drops sharply along the western coast. From the northern part of the western coast and then along the northern and south along the eastern coast the winter temperatures are low and do not vary much until the temperature boundary is reached. In summer (e.g. August) the temperatures decrease rather gradually from the southern coasts along the west till the northern coast is reached. From there

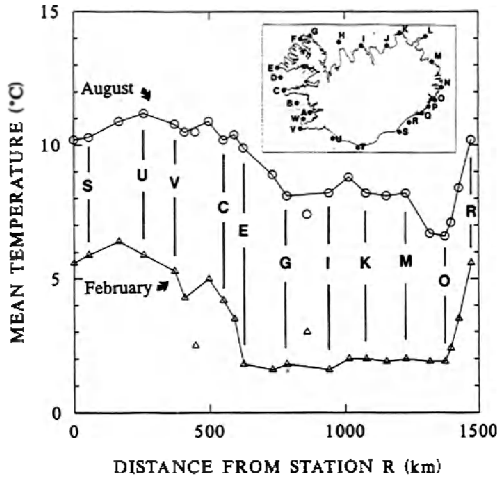

Fig. 2. Mean temperatures for August and February, 1949-1966, at 23 coastal stations, A-W, around Iceland, from Stefánsson 1969. Two of his stations, A and H, are shown unconnected with the remainder. Station A was at the innermost part of a bay and showed unusually low winter temperatures while station H was located far offshore and showed exceptionally high winter and low summer temperatures. Distances were measured between adjacent stations and then summed cumulatively clockwise around Iceland from station R, located just south of the temperature boundary off southeastern Iceland. Inset shows positions of stations.

the temperature remains similar until there is a drop going south along the eastern coast. The middle part of the eastern coast is cooler in summer than any other part. Sharpish temperature boundaries thus occur in the following regions: southeastern coasts (all seasons), middle part of western coast (winter only) and, to a lesser degree, the middle part of the eastern coast (summer only). A less abrupt change is seen along the northwestern coast in summer.

The sea may freeze in winter in the innermost parts of bays and sheltered fjords. Arctic sea ice sometimes drifts up to the northern and eastern coasts and remains for months packed against the shores. The last severe ice year was in 1968 (Eythorsson & Sigtryggsson 1971).

Air temperatures at coastal stations in Iceland generally decline from south to north (Eythorsson & Sigtryggsson 1971) on both western and eastern coasts. In summer, however, the temperatures along the east coast are 1-2° C lower than at corresponding latitudes on the west coast and similar to temperatures on the north coast. Average July temperatures range from a little more than 11° C in the South to a little above 8° C in the north and east, while average January temperatures range from about 1-2° C in the extreme south to a little less than -2° C in the north.

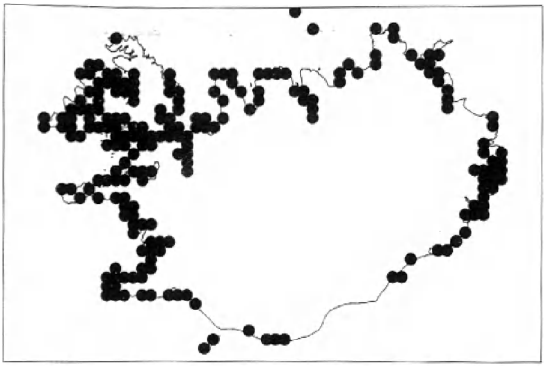

Fig. 3. The 208 squares, each 10 x 10 km, from which data on intertidal macrofauna are available.

RESULTS

Data are available for 208 of the 378 coastal squares, or 55.0 % (Fig. 3). The total number of identified species was 163. A list of these species together with authors' names is given in the Appendix. Species numbers in studied squares varied from 0-70 (mean: 20.4; mode: 20; SD: 13.3) and showed a good log-normal distribution, but with a 'tail' of some 29 squares with only 0-3 species recorded. Most but not all are squares where no systematic surveys have been done. The three squares with the highest number of species (57, 58, and 70 species) are in the Reykjavík region, southwestern Iceland, where the sampling effort is greater than elsewhere. When groups that were only occasionally identified to species are omitted (Porifera, most Hydrozoa, Bryozoa, Oligochaeta, Araneida, most Insecta, Nemertea, and Opistobranchia) as well as subtidal species which are only rare stragglers to the intertidal (all recorded from 4 squares or less) and the stickleback (*Gasterosteus aculeatus*) (omitted because it did not fit any category used for analysis) the number of species (or more strictly, taxa) remaining was 103. This includes all species identified from five or more squares, except one Porifera and the stickleback (each identified from six squares), as well as six species recorded from less than five squares. These are either species confined to the intertidal (*Ligia oceanica*, *Manayunkia aestuarina*) or species recorded from 2-4 squares lying close together (*Echiurus echiurus*, *Halicryptus spinulosus*, *Idotea neglecta*, and *Pycnogonum littorale*).

Most species recorded from the intertidal zone in Iceland may by divided with relative ease among two groups, i.e. species confined to the intertidal or virtually so (obligate intertidal species), and species, usually vagile ones, also found in the subtidal (intertidal/subtidal species). The allotting of species to groups is based primarily on own experience (see Ingólfsson 1975, 1992) augmented with advice from several experts as well as information from the literature. The allotting of a few species may, however, be questionable, but I do not think that this can materially affect the main results. Both groups may be subdivided according to preferred substrate into hard-bottom and soft-bottom species. In the following, therefore, four species groups will be treated.

Obligate intertidal species

The number of well-known obligate intertidal species preferring hard substrates is 27 although a few are difficult to classify according to substrate preference. The two gastropod species *Littorina obtusata* and *L. mariae* are here treated as one, referred to as *L. obtusata*, as they have usually not been differentiated in analysis of samples.

Twenty-two of these have been recorded on all coasts (Table 1). Fig. 4 gives three examples. All are, however, absent from large stretches of the south coast due to lack of suitable substrate. The remaining five species are clearly confined to the warmer coastal regions of Iceland (Fig. 4). In the following the number of squares in which species have been recorded is shown in parenthesis after the names. Going clockwise around the island starting on the south coast, the first species to drop out is the isopod *Ligia oceanica* (three squares). The distribution of this species in Iceland is remarkably limited. The one locality where it is abundant (the westernmost) is geothermally heated a few degrees above the surroundings. The amphipod *Orchestia gammarella* (11) extends only a little further along the coast with the exception of two outliers, where the species is confined to the vicinity of hot springs opening in the intertidal. The amphipod *Gammarus marinus* (27) is the next species to drop out followed by the isopod *Idotea pelagica* (27) which reaches to the middle part of the northern coast at least, and finally, the gastropod *Nucella lapillus* (87) is only absent from the middle part of the eastern coast. The isopod *Idotea pelagica* shows an anomaly in its pattern in that it has been recorded from Hvalnes, a locality in the southernmost part of the eastern coasts on the cool side of the temperature boundary. The species has also been recorded from the islands of Hrollaugseyjar which are on the warm side of the boundary some 85 km to the south.

There are some ten obligate intertidal species preferring soft substrates. The distributional pattern shown by these can be expected to be discontinuous to a greater degree than that of the hard-bottom species, as suitable substrate is unevenly dispersed along the coast. Six of the species are found on all coasts (Table 1) except the major part of the south coast where suitable substrate is lacking. Fig. 5

gives three examples. The remaining four appear to be confined to the warmer parts of the coast (Fig. 5). Going clock-wise around Iceland from the south the first species to drop out is the polychaete *Manayunkia aestuarina* (four squares), which is confined to the southwest. The gastropod *Hydrobia ventrosa* (seven) and the bivalve *Cerastoderma edule* (nine) occur along the whole west coast, while the amphipod *Corophium bonelli* (11) has been recorded in addition along the greater part of the north coast, although localities are widely dispersed.

In all nine of the 37 obligate intertidal species (24 %) appear to reach distributional limits towards cooler seas within Iceland, while there is no example of such species reaching distributional limits towards warmer seas.

Intertidal/subtidal species

Of the total number of 66 species included in this group about 40 are found mostly on hard substrates, including

Table 1. Macrofaunal species recorded from the intertidal on all coasts where suitable substrate is found. The number of 10 x 10 km squares in which the species have been recorded of the total of 208 examined is shown. Symbols: (a) = Amphipoda, (an) = Anthozoa, (b) = Bivalvia, (c) = Cirripedia, (d)= Decapoda, (g) = Gastropoda, (h) = Hydrozoa, (i) = Isopoda, (in) = Insecta, (m) = Mysidacea, (p) = Polychaeta.

Obligate intertidal species	Number of squares	Species found intertidally and subtidally	Number of squares
Hard substrate:		Hard substrate:	
Littorina saxatilis (g)	154	*Mytilus edulis* (b)	154
Littorina obtusata (g)	148	*Tectura testidunalis* (g)	90
Gammarus oceanicus (a)	134	*Naineris quadricuspida* (p)	89
Semibalanus balanoides (c)	132	*Margarites helicinus* (g)	89
Skeneopsis planorbis (g)	126	*Ampithoe rubricata* (a)	76
Gammarus obtusatus (a)	119	*Calliopius laeviusculus* (a)	70
Idotea granulosa (i)	114	*Lacuna vincta* (g)	66
Fabricia sabella (p)	113	*Lacuna pallidula* (g)	55
Hyale nilssoni (a)	112	*Gammarellus homari* (a)	39
Onoba aculeus (g)	108	*Hyas araneus* (d)	31
Halocladius variabilis (in)	105	*Urticina felicina* (an)	30
Turtonia minuta (b)	96	*Nereis pelagica* (p)	20
Gammarus duebeni (a)	82	*Caprella septentrionalis* (a)	19
Jaera albifrons (i)	75	*Mysis oculata* (m)	5
Gammarus setosus (a)	65		
Micralymma marinum (in)	61		
Gammarus finmarchicus (a)	59	Soft substrate:	
Jaera prehirsuta (i)	59	*Eteone longa* (p)	43
Gammarus stoerensis (a)	57	*Capitella capitata* (p)	38
Jaera ischiosetosa (i)	52	*Cirratulus cirratus* (p)	32
Dynamena pumila (h)	31	*Phyllodoce maculata* (p)	17
Spirorbis spirorbis (p)	22	*Eulalia viridis* (p)	15
Soft substrate:			
Arenicola marina (p)	69		
Pygospio elegans (p)	69		
Gammarus zaddachi (a)	45		
Onisimus litoralis (a)	39		
Mya arenaria (b)	34		
Hediste diversicolor (p)	29		

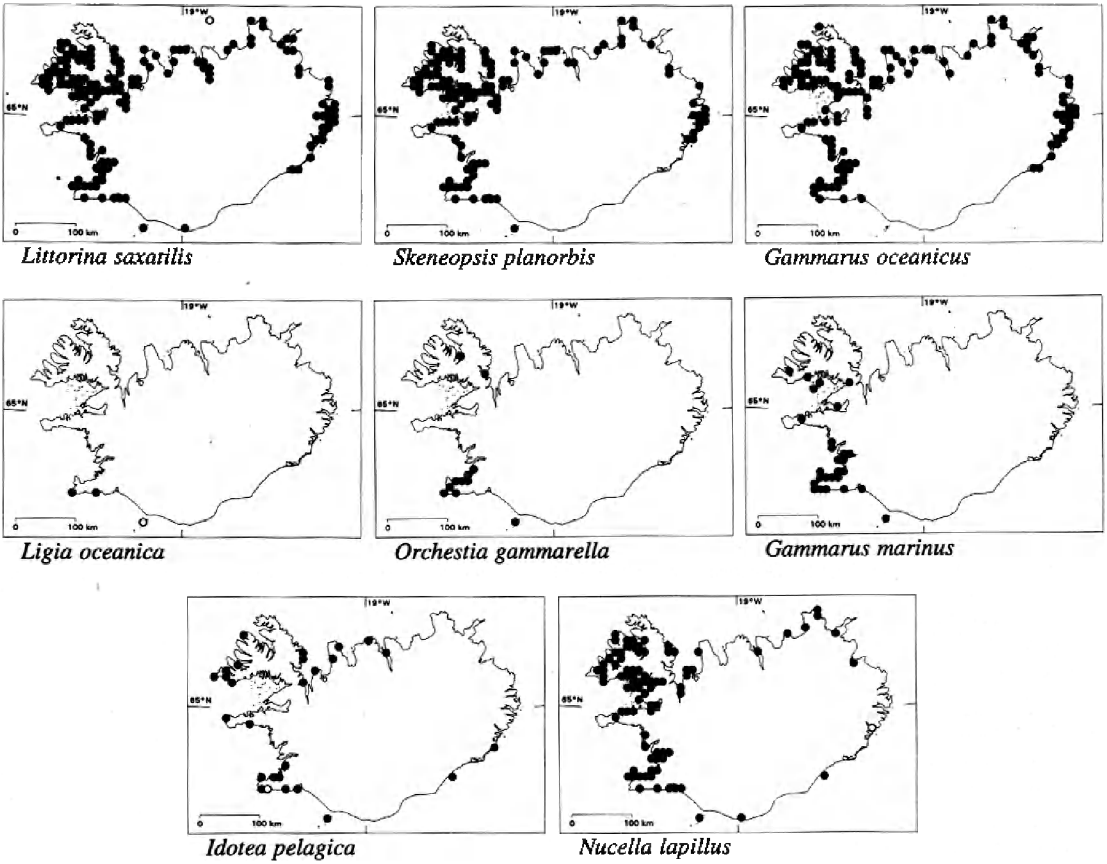

Fig. 4. Distribution of obligate intertidal species preferring hard substrates. Top row: Examples of species common on all coasts where suitable substrate is found. Remainder: Five species showing distributional limits towards cooler temperatures within Iceland. Open circles denote pre-1960 records.

the hyperbenthic mysids *Mysis oculata* and *Praunus flexuosus*. Many of these hard-bottom species are common and even dominant in the intertidal, especially the lowermost part. Fourteen species are found on all coasts where suitable habitats are present and most are common (Table 1). Fig. 6 gives three examples. The remaining 26 species have been recorded in the intertidal only on certain coasts. With one exception these species are lacking or almost so from the intertidal on the colder coasts. Some are confined to the southwest (the pycnogonid *Pycnogonum littorale* (three squares, Fig. 7), the amphipod *Apherusa jurinei* (three, Fig. 6), the isopod *Idotea neglecta* (four, Fig. 6), the gastropod *Ansates pellucidum* (eight, Fig. 7), and the asteroid *Henricia sanguinolenta* (seven, Fig. 7)). Others have also been recorded up to the middle of the west coast (the mysid *Praunus flexuosus* (nine, Fig. 6), the asteroid *Asterias rubens* (eight, Fig. 7) and the decapod *Carcinus maenas* (13, Fig. 6)) or along the whole west coast (the amphipod *Parajassa pelagica* (11, Fig. 6), the barnacle *Balanus crenatus* (ten, Fig. 6), the lumpsucker (*Cyclopterus lumpus* (seven)), the butterfish (*Pholis gunnellus* (11)), the hermit crab *Pagurus bernhardus* (eight), the bivalve *Modiolus modiolus* (ten, Fig. 7), and the chiton *Stenosemus albus* (five, Fig. 7)). Many species extend in addition along the north coast to varying degrees (in order of extent: the amphipod *Dexamine thea* (14, Fig. 6), the gastropod *Omalogyra atomus* (33, Fig. 6), the gastropod *Buccinum undatum* (39, Fig. 7), the bivalve *Hiatella arctica* (18, Fig. 7), the pycnogonid *Phoxichilidium femoratum* (15, Fig. 7), the amphipod *Gammarus locusta* (7, Fig. 6), the isopod *Idotea emarginata* (13, Fig. 6), and the polychaete *Harmothoe imbricata* (17, Fig. 7)). Finally, the isopod *Idotea baltica* (31, Fig. 6) extends in addition some ways south along the east coast. The bivalve

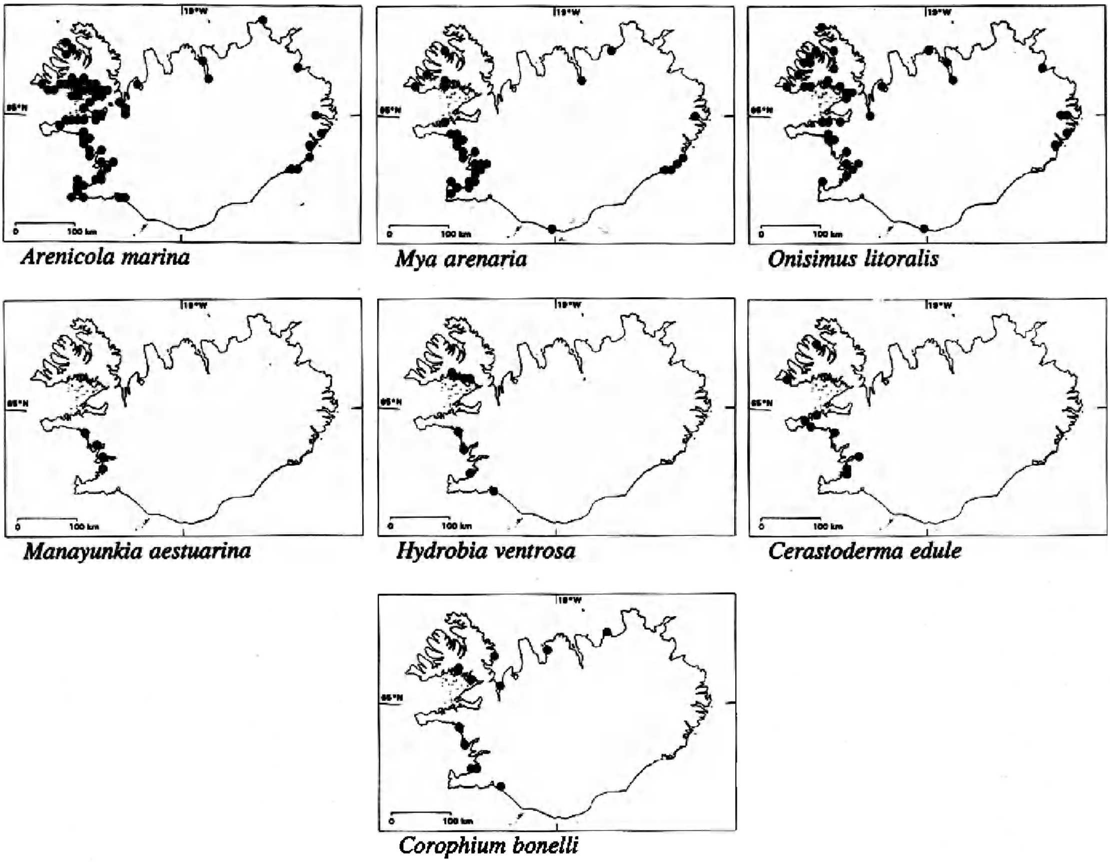

Fig. 5. Distribution of obligate intertidal species preferring soft substrates. Top row: Examples of species common on all coasts where suitable substrate is found. Remainder: Four species showing distributional limits towards cooler temperatures within Iceland.

Musculus discors (33, Fig. 7) also belongs with these species, except for an isolated record in the middle part of the east coast. It should be noted that both *Modiolus modiolus* and *Buccinum undatum* also have isolated outlying records far removed from their main intertidal ranges described above (Fig. 7). There is only one species in this group, the amphipod *Ischyrocerus anguipes* (28, Fig. 7), which is common on the colder eastern and northern coasts, while almost lacking from the intertidal in the warmer middle west and southwest.

The amphipod *Parajassa pelagica* shows a similar anomaly in its distribution as the isopod *Idotea pelagica*, mentioned above. Both species have been recorded on the cool side of the temperature boundary on the southeast coast, although being otherwise confined to warmer coasts. Both have also been recorded from a locality on the warm side of the boundary, some 85 km to the south.

About 26 of the intertidal/subtidal species prefer soft substrates. Some five of these have been recorded rather commonly from all coasts where suitable substrate is found (Table 1). Fig. 8 gives three examples. Most, however, appear to be confined or largely so to the intertidal of the warmer coasts, where they are often quite common. The polychaetes *Nereis virens* (five squares, Fig. 8) and *Ophelia limacina* (six, Fig. 8) and the echiurid *Echiurus echiurus* (two) have only been found in the southwest. Although recorded only from two squares repeated sampling have shown the intertidal populations of *E. echiurus* to be permanent. The polychaetes *Pectinaria koreni* (six, Fig. 8), *Brada villosa* (seven), and *Brada inhabilis* (ten, Fig. 8), and the amphipod *Anonyx sarsi* (six) appear confined to southwestern and middle western coasts. The amphipod *Pontoporeia femorata* (14, Fig. 8) is similar but with outliers in the southeast near the temperature boundary. The

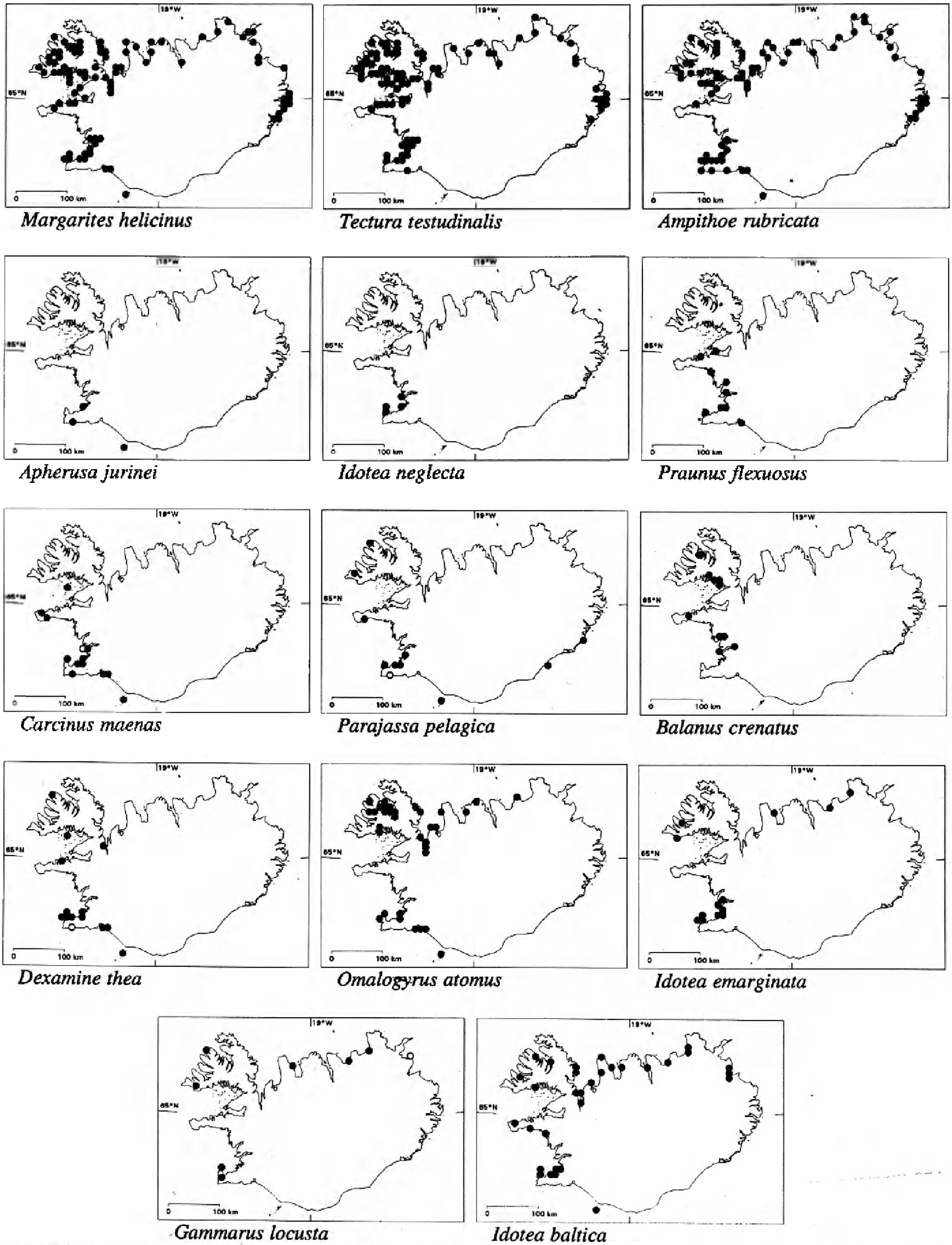

Fig. 6. Intertidal distribution of species found both intertidally and subtidally and preferring hard substrates. Top row: Examples of species common on all coasts where suitable substrate is found. Remainder: Eleven species showing distributional limits towards cooler temperatures within Iceland. These 11 species are not known to penetrate deeper into cooler seas subtidally than intertidally. Open circles denote pre-1960 records.

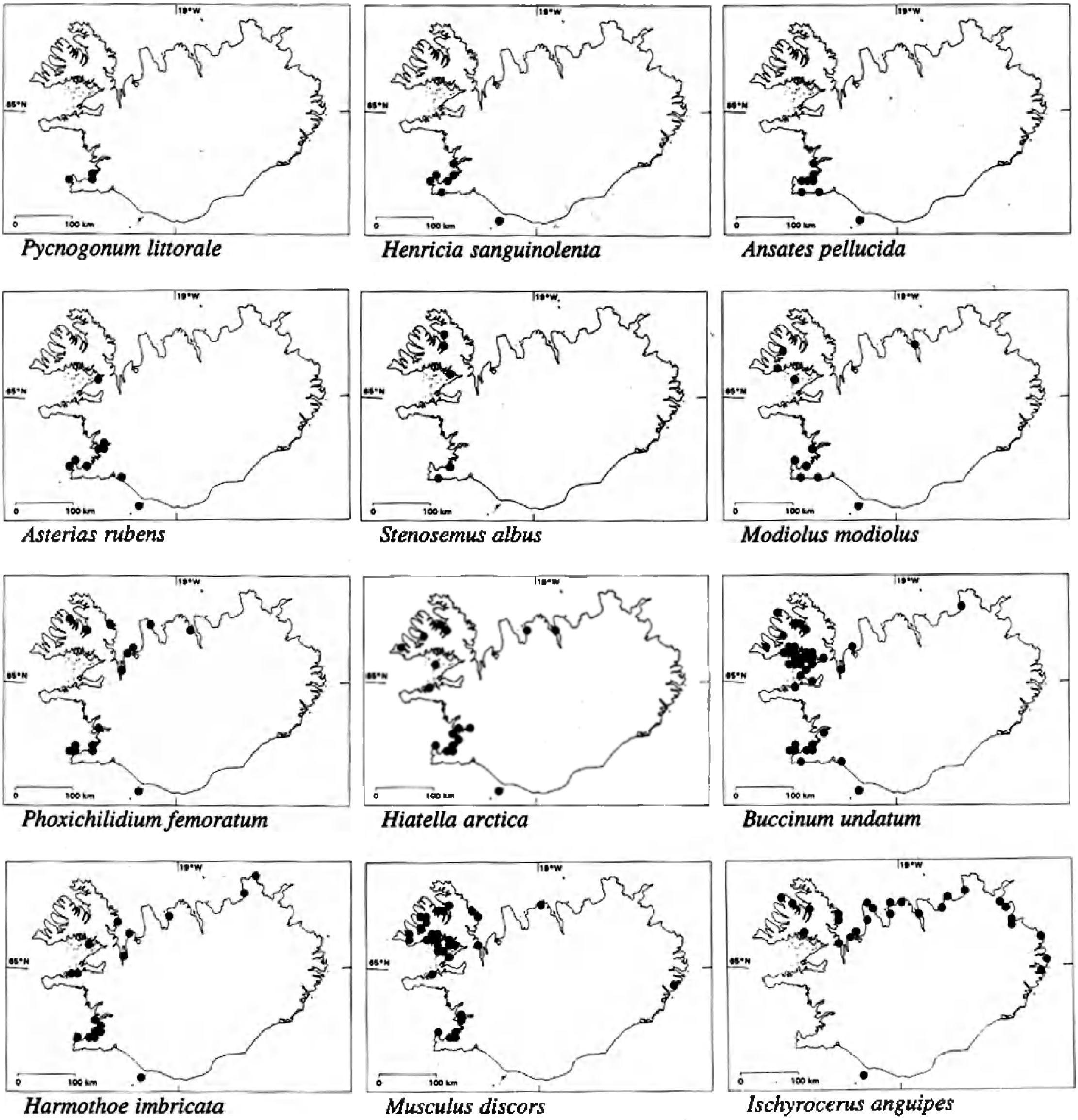

Fig. 7. Intertidal distribution of 12 species found subtidally all around Iceland (except *Ansates pellucida*) but intertidally virtually limited to the warmer or the colder (*Ischyrocerus anguipes*) coasts of the island. All species shown prefer hard bottoms.

bivalves *Macoma calcarea* (14, Fig. 8) and *Mya truncata* (eight, Fig. 8) and the polychaetes *Travisia forbesi* (14, Fig. 8) and *Malacoceros vulgaris* (six, Fig. 8) have additionally been found on northwestern coasts, while the priapulid *Priapulus caudatus* (28, Fig. 8) and the polychaetes *Scalibregma inflatum* (12, Fig. 8) and *Pholoe* sp. (five) extend to the westernmost part of the north coast. The polychaete *Scoloplos armiger* (38, Fig. 8) shows a similar pattern but with an outlying record in southeastern Iceland near the temperature boundary. The polychaete *Spio filicornis* (12) has two outlying records outside the west coast, i.e. in the middle north and the northeast. Due to taxonomic difficulties polychaetes of the genus *Polydora* were not always identified to species. At least two species

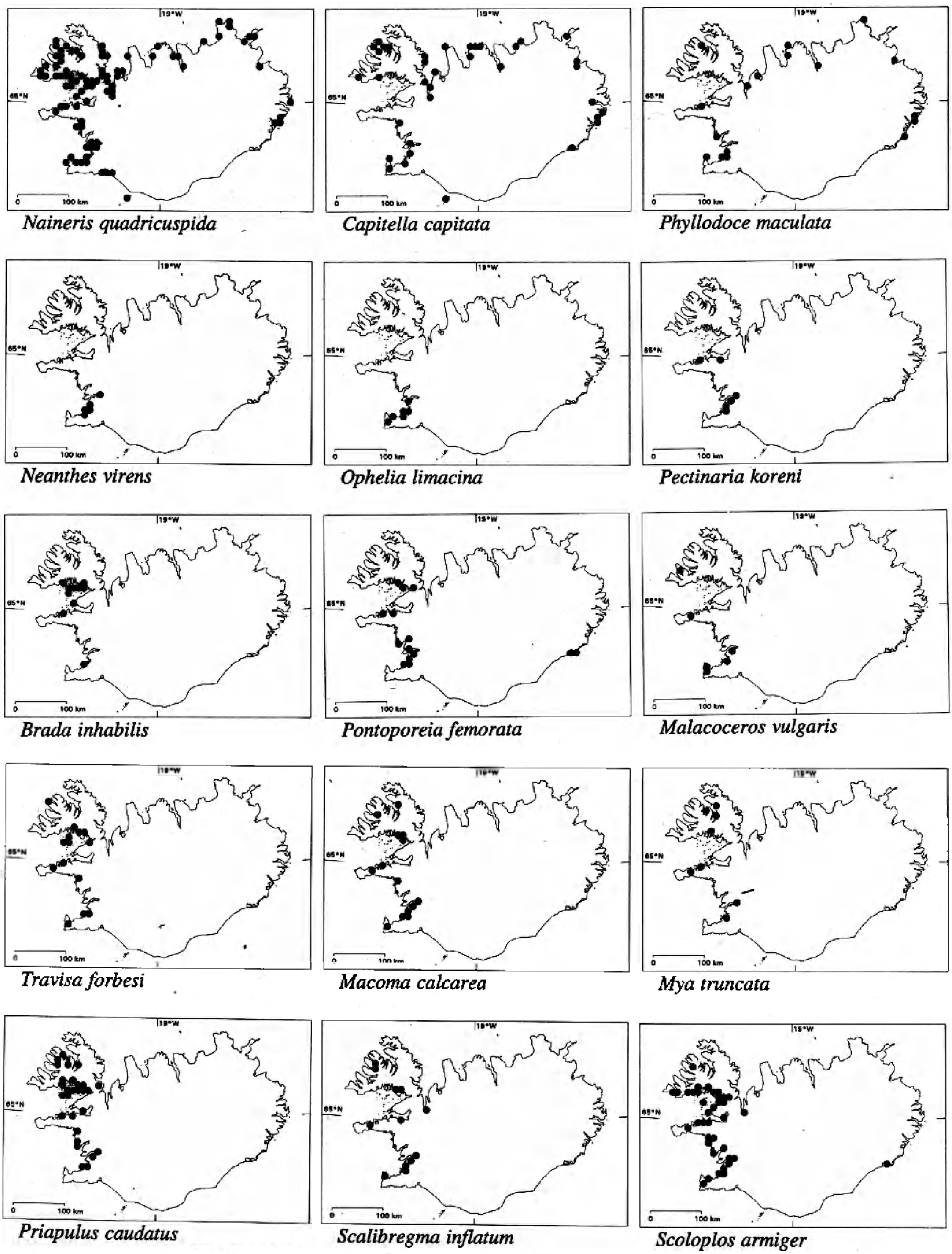

Fig. 8. Intertidal distribution of species found both intertidally and subtidally and preferring soft substrates. Top row: Examples of species common on all coasts where suitable substrate is found. Remainder: Twelve species found subtidally all around Iceland but intertidally virtually limited to the warmer coasts of the island.

were involved, *Polydora quadrilobata* and *P. ciliata*. *Polydora* spp. were found in 45 squares, on all coasts except the east. The priapulid *Halicryptus spinulosus* (two) has only been found in two adjoining squares in the south-east. The polychaete *Ophryotrocha puerilis* (seven) is rather aberrant, as the records all lie on the northern and northwestern coast. It is a tiny species and may have been overlooked elsewhere. No additional soft-bottom species of this group have been recorded in five or more squares but the number of such species recorded sporadically from the intertidal (from 1-4 squares) is high.

In all some 46 of the 66 (67 %) intertidal-subtidal species appear to reach distributional limits in the intertidal, all except two towards cooler seas.

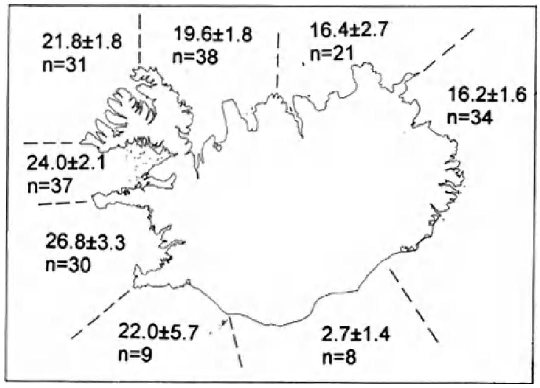

Fig. 9. Mean number of species recorded from 10 x 10 km squares in different parts of the shoreline of Iceland, shown with standard error and the number of squares examined.

Species numbers

The average total number of species recorded per square drops steadily clockwise around Iceland from a high of 26.8 in the Faxaflói region in the southwest to 16.2 on the east coast (Fig. 9). The low mean of 2.7 for the exposed sandy south coast is due to a number of squares examined with zero or one species. The trends are not so clear when obligate intertidal species are analysed separately, although the average recorded number of such species is higher on the west coast (means with standard errors: 14.4 ± 1.5 (n = 30), 13.8 ± 1.1 (n = 37) and 15.3 ± 1.1 (n = 31) for the three regions shown in Fig. 9, respectively) than on the north (12.6 ± 1.0 (n =38), 11.5 ± 1.8 (n = 21), respectively) and east coasts (11.0 ± 1.0 (n = 34).

DISCUSSION

The emerging pattern is of numerous species, both obligate intertidal ones and those also occurring in the subtidal, dropping out as one moves clockwise around Iceland from the South with few if any replacements by northern species.

In addition to the nine obligate intertidal species that exhibit clear distributional limits towards cooler seas the following 11 intertidal-subtidal species also do so in the intertidal, without apparently penetrating deeper into cooler seas subtidally: *Apherusa jurinei*, *Idotea neglecta*, *Omalogyra atomus*, *Balanus crenatus*, *Praunus flexuosus*, *Carcinus maenas*, *Parajassa pelagica*, *Gammarus locusta*, *Idotea emarginata*, *I. baltica*, and *Dexamine thea* (Fig. 6). All are species confined to very shallow waters. When the 20 limits as they appear from the maps are plotted cumulatively on a graph also showing mean temperatures for the coldest (February) and warmest (August) months (Fig. 10), three sections appear to be distinguishable. The graph rises steeply (i.e. there are many limits) on the coastal section 100-200 km from station U (Vestmannaeyjar Islands) of Stefánsson (1969). Another steep rise can be seen between 300 and 500 km from station U. The first steep rise is quite possibly due to the high level of sampling in the Reykjavík area. The second steep rise coincides well with a rather steep decline of summer temperatures, but appears to extend over a larger area than the abrupt drop in winter temperature along this coastal section. Surprisingly, the cumulative graph continues to rise steadily between 500 and 900 km from station U, although temperatures do not change noticeably along this stretch. The possibility cannot be excluded that actual limits in some cases (e.g. *Gammarus locusta*, only recorded from six squares) lie further along the coast, undetected because of insufficient sampling. The two species that reach their limits last do so apparently about where the drop in summer temperatures occurs.

The northern limits of the amphipod *Orchestia gammarella*, both in Norway, Iceland and eastern Canada, lie in relatively warm waters (Ingólfsson 1977a). Its occurrence in two spots far distant from its main area of distribution in Iceland (Fig. 5), both under the influence of warm springs, convincingly demonstrates the temperature limitation of the species. The two isolated warm-spring populations are probably better explained as relicts of a former wider distribution than as results of dispersal from the present main area of distribution. The climate of Iceland was probably considerably warmer than now about 2500-4000 B.P. (Einarsson 1963), or 3400-4800 B.P. (Stötter 1991), and the distribution of many cold-sensitive species may then have been much wider than now.

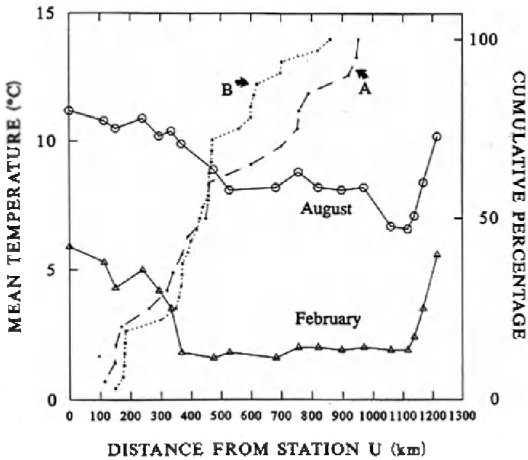

Fig. 10. The dispersion of distributional limits of two groups of species, A and B, in the intertidal towards colder seas shown with summer (August) and winter (February) temperatures. The graph shows cumulative numbers of limits as percentages of total number of limits. Groups A (20 limits) includes both obligate intertidal species and intertidal/subtidal species not extending further subtidally than they do intertidally. Group B (32 limits) consists of species with wider distribution subtidally than intertidally. One or two obviously outlying records in case of one species in group A (*Orchestia gammarella*) and four species in group B (*Musculus discors*, *Modiolus modiolus*, *Buccinum undatum*, *Spio filicornis*) are omitted (see text). Distances between adjacent stations are summed cumulatively clockwise around Iceland from station U of Stefánsson 1969 (see Fig. 2). Southeastern Iceland, where stations R, S, and T of Stefánsson are located, is omitted due to aberrant shore types (see Fig. 1).

It is somewhat unfortunate that the sharp temperature boundary on the southeastern coast is near the junction of radically different shore types, exposed sandy shores to the South and rocky shores and muddy tidal flats to the North (Fig. 1). However, there is an isolated group of small skerries, Hrollaugseyjar, just south of the boundary. The exposure is extreme, but nevertheless some intertidal species have been recorded, including three species, *Nucella lapillus*, *Idotea pelagica* and *Parajassa pelagica*, which reach distributional limits towards cooler seas in Iceland. Interestingly, *I. pelagica* and *P. pelagica* have been recorded also just north of the boundary as it normally lies (Fig. 5). As the boundary is known to fluctuate considerable in position (Stefánsson 1969) this is not totally unexpected. In addition, mobile animals can be expected to cross an unfavourable temperature boundary now and then, although a persistent population may not be established. Neither species has planktonic larvae but both have been recorded from drifting seaweed which may serve as a dispersal agent along the shores (Ingólfsson 1995). There is an old record of *Nucella lapillus* a little further north of the temperature boundary (Thorson 1941), which, if correct, may be explained in a similar fashion, although I know of no record of it on floating objects.

None of the 11 obligate intertidal species with distributional limits towards cooler seas within Iceland have been recorded from frigid Svalbard but, surprisingly, one of the nine subtidal-intertidal species where such limits in the intertidal appear to coincide with subtidal limits, i.e. *Balanus crenatus*. In contrast out of 24 obligate intertidal species found on all coasts in Iceland on which I have sufficient distributional information elsewhere 12 have been recorded from Svalbard (Stephensen 1937a, 1940; Thorson 1941; Madsen 1949; Wesenberg-Lund 1951; Larsson & Gígja 1959; Ingólfsson 1977a; Nilsson-Cantell 1978; Weslawski & al. 1993), reflecting the difference in temperature-requirements of the two groups (Fisher's Exact Test applied on proportion in Svalbard waters gives $P = 0.002$).

No examples are known of obligate intertidal species showing distributional limits towards warmer temperatures within Iceland. I am not aware of any macrofaunal intertidal species of the arctic Atlantic that does not reach south to Iceland. There is no arctic endemic element among intertidal macrofauna which contrasts with estimates of 5-14 % of the shallow benthic fauna of the arctic being endemic (Dunton 1992). Shores of the arctic are depauperate and often largely barren due to ice action (Ellis & Wilce 1961), and conditions there presumably not conducive to the evolution of new species. Only two of the 39 obligate intertidal species treated in the present paper are lacking from the much warmer shores of The British Isles, i.e. the amphipods *Gammarus setosus* and *Onisimus litoralis* (Lincoln 1979), further emphasizing the non-arctic character of the intertidal fauna.

One species, the priapulid *Halicryptus spinulosus*, is in Iceland, both intertidally and subtidally, confined to brackish lagoons in the cold southeast. Its distribution elsewhere is high-arctic except for populations in the Baltic and one or two other boreal localities (Van Der Land 1970). It is almost everywhere confined to brackish waters, but it is difficult to see what else than temperature prevents it from occurring in warmer lagoons in Iceland.

A large number of the subtidal-intertidal species here considered, or some 34 of the total of 64 (53%), show distributions in the intertidal more limited in geographical extent than their subtidal distributions. Their intertidal distribution is with one exception confined to warmer coasts than their subtidal one. Both hard-bottom (Fig. 7) and soft-bottom (Fig. 8) species are involved and most are common on all coasts subtidally (Einarsson 1948; Knudsen

1949; MADSEN 1949; SÆMUNDSSON 1949; STEPHENSEN 1937b, 1939, 1940; THORSON 1941; WESENBERG-LUND 1937, 1951). This pattern is probably due to low and variable air temperatures becoming more critical as the sea becomes cooler, preventing many species from surviving in the intertidal. Other possible hypotheses, e.g. ones relating the pattern to tidal regimes or to substrate, do not correlate well with the observed trends.

When the distribution limits in the intertidal of the 32 species (counting the polychaetes *Polydora quadrilobata* and *P. ciliata* as one) confined intertidally to the warmer coasts but having wider distributions subtidally are plotted cumulatively the resulting graph is very similar to that for the 11 obligate intertidal and 9 intertidal-subtidal species with coinciding intertidal and subtidal limits (Fig. 10). There are many limits, i.e. the graph rises steeply, in the Reykjavik area and then again in the area of rather steep decline of summer temperatures between 300 and 500 km from station U (Vestmannaeyjar). Limits continue, however, to be encountered in regions where temperatures are no longer decreasing. Most of the 33 species in question, or 23, are known to occur in Svalbard waters, reflecting their tolerance to low temperatures.

The intertidal pattern shown by species only common in the intertidal in part of their range can be expected to show anomalies not seen among species confined to the intertidal. Unusual conditions, occasional stragglers or sampling during exceptionally low tides can 'disrupt' otherwise distinct patterns. There are several examples of this, e.g. the bivalves *Modiolus modiolus* and *Musculus discors* (Fig. 7).

The amphipod *Ischyrocerus anguipes* (Fig. 7) shows an exceptional reversed patterns with virtual lack of intertidal records from the warmer coasts, although common subtidally there at shallow depths (STEPHENSEN 1940 and personal observations). This pattern is difficult to explain. This is not a pronounced cold-water species. In Britain, where sea temperatures are much higher, it occurs from low-tide level and down, but occasionally found intertidally in tide-pools (LINCOLN 1979).

ACKNOWLEDGEMENTS

The students, assistants and colleagues who have helped me in this work over the years in one way or another are much too numerous to mention here. Without their help very little would have been achieved. Dr. Helgi Gudmundsson, however, deserves special mention for his invaluable aid in the identification of polychaetes. Prof. Jörundur Svavarsson read an early version of this manuscript and made numerous constructive comments. I also thank Torleiv Brattegard and an anonymous reviewer for their many helpful suggestions.

REFERENCES

Anonymous. 1993. Sjávarföll við Ísland 1994. - *Sjómælingar Íslands* 41, 31 pp.

Astthorsson, O.S. 1987. Records and life history of *Praunus flexuosus* (Crustacea: Mysidacea) in Icelandic waters. - *Journal of Plankton Research* 9:955-964.

Dunton, K. 1992. Arctic biogeography: The paradox of the marine benthic fauna and flora. - *Trends in Ecology and Evolution* 7:183-189.

Einarsson, H. 1948. Echinodermata. - *The Zoology of Iceland.* IV, Part 70. 67 pp.

Einarsson, Th. 1963. Pollenanalytical studies on the vegetation and climate history of Iceland in late and postglacial times. - Pp. 355-365 in: Löve, A. & D. Löve (eds). *North Atlantic Biota and their History.* Pergamon Press, Oxford.

Ellis, D.V. & R.T. Wilce. 1961. Arctic and subarctic examples of intertidal zonation. - *Arctic* 14:224-235.

Eythorsson, J. & H. Sigtryggsson. 1971. The climate and weather of Iceland. - *The Zoology of Iceland.* I, Part 3. 62 pp.

Garðarsson, A., A. Ingólfsson, & J. Eldon. 1976. Lokaskýrsla um rannsóknir á óshólmasvæði Eyjafjarðarár 1974 og 1975. - *Líffræðistofnun Háskólans. Fjölrit* 7. 63 pp.

Garðarsson, A., Ó. K. Nielsen, & A. Ingólfsson. 1980. Rannsóknir í Önundarfirði og víðar á Vestfjörðum 1979. Fuglar og fjörur. - *Líffræðistofnun Háskólans. Fjölrit* 12. 65 pp.

Garðarsson, A., J. Pálsson, and A. Ingólfsson. 1974. Könnun og kortlagning lífríkis í suðurhluta Leiruvogs nærri Reykjavík. - *Líffræðistofnun Háskólans. Fjölrit* 2. 33 pp.

Hansen, J.R. and A. Ingólfsson. 1993. Patterns in species composition of rocky shore communities in sub-arctic fjords of eastern Iceland. - *Marine Biology* 117:469-481.

Hauksson, E. 1977. Distribution and habitat of marine littoral invertebrates in Breidafjördur, W-Iceland. - *Náttúrufræðingurinn* 47:88-98. (In Icelandic with English summary).

Hayward, P.J. & J.S. Ryland (eds). 1990. *The Marine Fauna of the British Isles and North-West Europe.* - Clarendon Press, Oxford. 996 pp.

Helgason, G.V., A. Ingólfsson, & A. Garðarsson. 1988. Könnun á leiru í Breiðdalsvík 1986. - Mimeographed manuscript. 19 pp.

Ingólfsson, A. 1973. *Orchestia gammarella* (Pallas) (Amphipoda: Talitridae) recorded from Iceland. - *Náttúrufræðingurinn* 43:170-174. (In Icelandic with English summary).

— 1975. Life on seashores - *Rit Landverndar* 4:61-99. (In Icelandic with English summary).

— 1976a. Forkönnun á lífríki Gilsfjarðar, Þorskafjarðar, Djúpafjarðar, Gufufjarðar og nærliggjandi fjarða. - *Líffræðistofnun Háskólans. Fjölrit* 8. 51 pp.

— 1976b. Zonal distribution of plants and arthropods on a salt marsh in SW. Iceland. - *Náttúrufræðingurinn* 46:223-237. (In Icelandic with English summary).

— 1977a. Distribution and habitat preferences of some intertidal amphipods in Iceland. - *Acta Naturalia Islandica* 25:1-28.

— 1977b. Rannsóknir í Skerjafirði. II. Lífríki fjöru. - *Líffræðistofnun Háskólans. Fjölrit* 10. 94 pp.

— 1983. Athuganir á lífríki fjöru í grennd við Grundartanga, Hvalfirði. - *Rannsóknir á lífríki fjöru og umhverfi við Grundartanga* 9. 96 pp.
— 1984. Athuganir á fjörum Skutulsfjarðar og annarra fjarða við Ísafjarðardjúp. - Mimeographed manuscript. 7 pp.
— 1986. Fjörulíf í innanverðum Dýrafirði. - *Líffræðistofnun Háskólans. Fjölrit* 24. 30 pp.
— 1990a. Nokkur orð um Þanglýs (*Idotea* spp.) í íslenskum og erlendum fjörum. - Pp. 9-12 in: Eggertsson, G, G F. Guðmundsson, R. Thorláksdóttir & S. Sigmundsson (eds). *Brunnur Lifandi Vatns.* Háskólaútgáfan, Reykjavík.
— 1990b. A survey of intertidal organisms around dumping pits for pot linings at Straumsvík, southwestern Iceland. - *Líffræðistofnun Háskólans. Fjölrit* 27b. 52 pp.
— 1991. Athuganir á lífríki fjöru við Álfsnes. - *Líffræðistofnun Háskólans. Fjörit* 31. 36 pp.
— 1992. The origin of the rocky shore fauna of Iceland and the Canadian Maritimes. - *Journal of Biogeography* 19:705-712.
— 1994. Species assemblages in saltmarsh ponds in western Iceland in relation to environmental variables. - *Estuarine, Coastal and Shelf Science* 38:235-248.
— 1995. Floating clumps of seaweed around Iceland: Natural microcosms and a means of dispersal for shore fauna. - *Marine Biology* 122:13-21.
Ingólfsson, A. & Á. Einarsson. 1980. Forkönnun á lífríki Nýpslóns og Skógalóns við Vopnafjörð. - *Líffræðistofnun Háskólans. Fjölrit* 15. 16 pp.
Ingólfsson, A. & A. Garðarsson. 1975. Forkönnun á lífríki Laxárvogs, Álftafjarðar og Önundarfjarðar. - *Líffræðistofnun Háskólans. Fjölrit* 4. 26 pp.
Ingólfsson, A. & K. Gunnarsson. 1984. Athuganir á gjám vestan Grindavíkur. - Mimeographed manuscript. 4 pp.
Ingólfsson, A. & G. V. Helgason. 1981. Athuganir lífríki Skógalóns við Vopnafjörð. - *Líffræðistofnun Háskólans. Fjölrit* 12. 26 pp.
Ingólfsson, A. & J. Svavarsson. 1989. Forkönnun á lífríki Gilsfjarðar. - *Líffræðistofnun Háskólans. Fjölrit* 26. 49 pp.
Ingólfsson, A., A. Kjartansdóttir, & A. Garðarsson. 1980. Athuganir á fuglum og smádýralífi í Skarðsfirði. - *Líffræðistofnun Háskólans. Fjölrit* 13. 21 pp.
Knudsen, J. 1949. Amphineura. - *The Zoology of Iceland.* IV, Part 59. 11 pp.
Kristinsson, H. & B. Jóhannsson. 1970. A grid system for the study of plant distribution in Iceland. - *Náttúrufræðingurinn* 40:58-65.(In Icelandic with English summary).
Larsson, S. G. & G. Gígja. 1959. Coleoptera 1. Synopsis. - *The Zoology of Iceland.* III, Part 46b. 218 pp.
Lindroth, C. H., H. Andersson, H. Bödvarsson & S. H. Richter. 1973. Surtsey, Iceland. The development of a new fauna, 1963-1970. Terrestrial invertebrates. - *Entomologica Scandinavica. Supplementum* 5:1-280.
Lincoln, R. J. 1979. *British Marine Amphipoda: Gammaridea.* - British Museum (Natural History), London. 658 pp.
Madsen, F.J. 1949. Marine Bivalvia. - *The Zoology of Iceland.* IV, Part 63. 116 pp.
Nilsson-Cantell, C.-A. 1978. *Cirripedia Thoracica and Acrothoracica. Marine Invertebrates of Scandinavia Number 5.* - Universitetsforlaget, Oslo. 135 pp.
Óskarsson, I., A. Ingólfsson & A. Garðarsson. 1977. *Hydrobia ventrosa* recorded in Iceland - *Náttúrufræðingurinn* 47:8-15. (In Icelandic with English summary).
Segerstråle, S. G. 1947. New observations on the distribution and morphology of the amphipod *Gammarus zaddachi* Sexton, with notes on related species. - *Journal of the Marine Biological Association of the United Kingdom* 27:219-244.
Solignac, M. 1972. Les *Jaera albifrons* d'Islande (Isopoda, Asellotes). - *Archives de Zoologie Experimentale et Generale* 113:433-437.
Steele, D.H. 1983. Marine ecology and zoogeography. - Pp. 421-465 in: South, G. R. (ed.). *Biogeography and Ecology of the Island of Newfoundland.* Dr. W. Junk Publishers, The Hague.
Stefánsson, U. 1969. Sjávarhiti á siglingaleið umhverfis Ísland. - Pp. 131-149 in: Einarsson M.Á. (ed.). *Hafísinn.* Almenna Bókafélagið, Reykjavík.
Stephensen, K. 1937a. Marine Isopoda and Tanaidacea. - *The Zoology of Iceland.* III, Part 27. 26 pp.
— 1937b. Pycnogonida.- *The Zoology of Iceland.* III, Part 58. 13 pp.
— 1939. Crustacea Decapoda. - *The Zoology of Iceland.* III, Part 25. 31 pp.
— 1940. Marine Amphipoda. - *The Zoology of Iceland.* III, Part 26, 111 pp.
Stötter, J. 1991. New observations on the postglacial history of Tröllaskagi, northern Iceland. - Pp. 181-191 in: Maizels, J.K. & C. Caseldine (eds). *Environmental Change in Iceland: Past and Present.* Kluwer Academic Publishers, Dordrecht.
Sæmundsson, B. 1949. Marine Pisces. - *The Zoology of Iceland.* IV, Part 72. 150 pp.
Thorson, G. 1941. Marine Gastropoda Prosobranchiata. - *The Zoology of Iceland.* IV, Part 60, 150 pp.
Van Der Land, J. 1970. Systematic zoogeography, and ecology of the Priapulida. - *Zoologische Verhandlungen* 112:1-122.
Wesenberg-Lund, E. 1937. Gephyrea. - *The Zoology of Iceland* II, Part 23. 16 pp.
— 1951. Polychaeta. - *The Zoology of Iceland* II, Part 19. 182 pp.
Weslawski, J., J. Wiktor, M. Zajaczkowski & S. Swerpel. 1993. Intertidal zone of Svalbard. 1. Macroorganism distribution and biomass. - *Polar Biology* 13:73-79.

Accepted 20 October 1995.

Appendix. Macrofaunal species identified from the intertidal of Iceland, in alphabetical order. The species marked with an asterisk (*) have been used in the analyses of distributional patterns.

Aeolidia pappilosa (L.)
Alderia modesta (Lovén)
Ammotrypane aulogaster Rathke
Ampharate acutifrons Grube
**Ampithoe rubricata* (Montagu)
Anomia squamula L.
**Anonyx sarsi* Steele & Brunel
**Ansates pellucida* (L.)
**Apherusa jurinei* Milne-Edwards
**Arenicola marina* (L.)
Arctica islandica (L.)
Aricidia jeffreysi (Mcintosh)
Astarte borealis Schumacher
**Asterias rubens* L.
Axinopsida orbiculata (Sars)
**Balanus crenatus* Bruguiére
Boreotrophon Clathratus (L.)
Boreotrophon truncatus (Ström)
**Brada inhabilis* (Rathke)
**Brada villosa* Rathke
**Buccinum undatum* L.
**Calliopius laeviusculus* (Krøyer)
**Capitella capitata* coll. (Fabricius)
**Caprella septentrionalis* Krøyer
**Carcinus maenas* (L.)
**Cerastoderma edule* (L.)
Chaetozone setosa Malmgren
Ciliatocardium ciliata (Fabricius)
**Cirratulus cirratus* (O.F. Müller)
Clitellio arenarius Müller
**Corophium bonelli* Sars
Crenella decussata (Montagu)
**Cyclopterus lumpus* L.
Dendronotus frondosus (Ascanius)
**Dexamine thea* Boeck
**Dynamena pumila* (L.)
**Echiurus echiurus* (Pallas)
**Eteone longa* (Fabricius)
Eualus gaimardi (Milne-Edwards)
**Eulalia viridis* (L.)
**Fabricia sabella* (Ehrenberg)
Flustrellida hispida (Fabricius)
**Gammarellus homari* (Fabricius)
**Gammarus duebeni* Liljeborg
**Gammarus finmarchicus* Dahl
**Gammarus locusta* (L.)
**Gammarus marinus* (Leach)
**Gammarus obtusatus* Dahl
**Gammarus oceanicus* Segerstråle
**Gammarus setosus* Dementieva
**Gammarus stoerensis* (Reid)
**Gammarus zaddachi* Sexton
Gasterosteus aculeatus L.
Halichondria panicea (Pallas)
**Halicryptus spinulosus* V. Siebold
Haliragus fulvocinctus (M. Sars)
**Halocladius variabilis* (Staeger)
**Harmothoe imbricata* (L.)
**Hediste diversicolor* (O.F. Müller)
**Henricia sanguinolenta* (O.F. Müller)
Heteromastus filiformis (Claparède)
**Hiatella arctica* (L.)
**Hyale nilssoni* (Rathke)
**Hyas araneus* (L.)
**Hydrobia ventrosa* (Montagu)
**Idotea baltica* Pallas
**Idotea emarginata* (Fabricius)
**Idotea granulosa* Rathke
**Idotea neglecta* Sars
**Idotea pelagica* Leach
**Ischyrocerus anguipes* Krøyer
**Jaera albifrons* Leach
**Jaera ischiosetosa* Forsman
**Jaera prehirsuta* Forsman
**Lacuna pallidula* (Da Costa)
**Lacuna vincta* (Montagu)
Lanice conchilega (Pallas)
Lanome kröyeri Malmgren
Laomedea flexuosa Alder
Laomedea longissima (Pallas)
Lepidonotus squamatus (L.)
**Ligia oceanica* L.
Limnephilus affinis Curtis
**Littorina mariae* Sacchi & Rastelli
**Littorina obtusata* (L.)
**Littorina saxatilis* (Olivi)
**Macoma calcarea* (Chemnitz)
**Malacoceros vulgaris* (Johnston)
**Manayunkia aestuarina* (Bourne)
Margarites groenlandicus (Gmelin)
**Margarites helicinus* (Fabricius)
Mediomastus fragilis Rasmussen
**Micralymma marinum* Ström
**Modiolus modiolus* (L)
**Musculus discors* (L.)
Musculus niger (Gray)
**Mya arenaria* L.
**Mya truncata* L.
Mysis mixta Liljeborg
**Mysis oculata* (Fabricius)
**Mytilus edulis* L.
Myxocephalus scorpius (L.)
**Naineris quadricuspida* (Fabricius)
Natica clausa Broderip & Sowerby
**Neanthes virens* (M.Sars)
Nebalia bipes (Fabricius)
**Nereis pelagica* L.
**Nucella lapillus* (L.)
**Omalogyra atomus* (Philippi)
Onchidoris fuscus (O. F. Müller)
Onchidoris muricata (O.F. Müller)
Onisimus edwardsi Krøyer
**Onisimus litoralis* (Krøyer)
**Onoba aculeus* (Gould)

Appendix. (continued). Macrofaunal species identified from the intertidal of Iceland, in alphabetical order. The species marked with an asterisk (*) have been used in the analyses of distributional patterns.

**Ophelia limacina* (Rathke)
Ophryotrocha bacci PARENTI
**Ophryotrocha puerilis* (CLAPARÈDE & MECZNIKOV)
**Orchestia gammarella* (PALLAS)
Owenia fusiformis Delle Chiaje
**Pagurus bernhardus* (L.)
**Parajassa pelagica* (LEACH)
Paranais litoralis (MÜLLER)
**Pectinaria koreni* MALMGREN
Petrobius marinus (LEACH)
**Pholis gunnellus* (L.)
**Pholoe* sp.
**Phoxichilidium femoratum* (RATHKE)
Phoxocephalus holboelli (KRØYER)
**Phyllodoce maculata* (L.)
**Polydora ciliata* (JOHNSTON)
**Polydora quadrilobata* JACOBI
**Pontoporeia femorata* KRØYER
Porcellio scaber LATREILLE
**Praunus flexuosus* (O.F.MÜLLER)
Praxilella praetermissa (MALMGREN)
**Priapulus caudatus* LAMARCK
Protomedeia fasciata KRØYER
Puncturella noachina (L.)
**Pycnogonum littorale* (STRØM)
**Pygospio elegans* (CLAPARÈDE)
Rhodine gracilior TAUPER
**Scalibregma inflatum* RATHKE
Scolelepis fuliginosa (CLAPARÈDE)
**Scoloplos armiger* (O.F. MÜLLER)
**Semibalanus balanoides* (L.)
Serripes groenlandicus (BRUGUIERE)
**Skeneopsis planorbis* (FABRICIUS)
**Spio filicornis* (O.F. MÜLLER)
**Spirorbis spirorbis* (L.)
**Stenosemus albus* (L.)
Strongylocentrotus droebachiensis (O.F. MÜLLER)
Syllis armilllaris (O.F. MÜLLER)
Syllis cornuta RATHKE
**Tectura testudinalis* (MÜLLER)
Terebellides stroemi M. SARS
Thyasira flexuosa (MONTAGU)
Tonicella rubra (L.)
**Travisia forbesi* JOHNSTON
Tubifex costatus (CLAPARÈDE)
Tubificoides benedine UDEKEM
**Turtonia minuta* (FABRICIUS)
**Urticina felina* (L.)
Verruca stroemia (O.F. MÜLLER)